

Biology of *Tricholabiodes* Radoszkowski in Southern Africa, with a New Synonymy and Review of Recent Biological Literature (Hymenoptera: Mutillidae)

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Abstract.—Papers dealing with the biology of Mutillidae since the last survey (Brothers 1989) are cited. *Tricholabiodes* Radoszkowski is the only genus of nocturnal Mutillidae recorded from southern Africa. Aspects of the biology of three species, *T. thisbe* (Péringuey) (= *T. carinifera* Bischoff *syn. nov.*), *T. livida* André and *T. imbellis* (André) (grooming), are described, based on field and laboratory observations in South Africa and Namibia. The following aspects are discussed: habitat, times of activity, predators and defence, mating, stridulation (during distress, copulation and as apparent communication) and grooming. This is the first account of the biology of any species in the genus.

INTRODUCTION

Although the Mutillidae comprises about 8000 species of sexually dimorphic wasps (female always wingless and male almost always winged), knowledge of their basic biology is very limited. Of the more than 200 papers dealing with mutillid biology, host-parasite relationships or life-history information, fewer than 20 report detailed studies of their biology (Brothers 1972, 1975, 1989). Since the last paper cited, the following papers have appeared: a review of mutillid adaptations (Deyrup 1988); information on water loss in *Dasylabris* sp. (Zachariassen *et al.* 1988); biological information on *Dasymutilla pyr-rhus* (Fox) (Manley & Deyrup 1989), *D. scaevola* (Blake) (Hook & Evans 1991) and *Pseudomethoca* species (Krombein 1992); details on copulation of *Myrmilla calva* f. *distincta* (Lepeletier) and *Myrmilla erythrocephala* f. *bison* (Costa) (Monastra 1989); seasonal flight activities of species of *Ephuta* Say, *Photomorphus* Viereck, *Pseudomethoca* Ashmead, *Sphaerophthalma* Blake and *Timulla* Ashmead (Deyrup & Manley 1990); observations on host associations

(e.g., Callan 1991, 1993, Krombein 1991, Riddick 1991, Brothers 1994, Yanega 1994, Weaving 1994, 1995, Neff & Rozen 1995); the effects of urbanization on Mutillidae (Gayubo & Torres 1989); and sex associations and mating behaviour (Cambra & Quintero 1993, Quintero & Cambra 1994).

Tricholabiodes (Sphaerophthalminae, Dasy-labriini), one of several genera of nocturnal mutillid wasps, is restricted to the arid and semi-arid regions of Africa and the Palaearctic. Its distribution in southern Africa includes all four desertic biomes: Nama Karoo, Succulent Karoo, Desert and arid parts of Savanna, which represent more than half of the area of the subcontinent, covering the western coastal belt between 12°S and 33°S and extending into the Kalahari basin and central Karoo plateau as far as about 26°E (Lovegrove 1993; Rutherford & Westfall 1994). This paper provides the first account of aspects of the biology of any species of the genus.

Specimens of *Tricholabiodes* are 3–12 mm long, with the mesosoma completely testaceous; males have large ocelli, hyaline wings with the forewings infuscated dis-

tally and a sparsely setose petiolate metasoma; females have the metasoma petiolate to sessile. Three species, *T. thisbe* (♂ & ♀), *T. livida* (♂ & ♀) and *T. imbellis* (♂), are treated (figs. 1–5). Identifications of males were made by comparison of voucher specimens with the holotypes or lectotypes, and of females by direct observation of sex associations (see below). As a consequence of such observations, the following new synonymy was established: *T. thisbe* (Péringuey 1898) (based on males only) = *T. carinifera* Bischoff 1920 (based on female only), *syn. nov.*, male observed *in copula* with female. (The female was identified by reference to the original description with which it agrees well; this is the only female found in southern Africa which has the very characteristic strong longitudinal ridges on the second metasomal tergum.) The genus is currently being revised by Bayliss & Brothers, and taxonomic details will be published later.

MATERIALS AND METHODS

Field observations were made during January to March 1995 and in January 1996 in the south-central and northwestern regions of South Africa, and in central Namibia; laboratory and field observations were made at Gobabeb Research Station, Namibia. In the field, a lighted dome (Oberprieler 1984) (with three centrally placed fluorescent tubes emitting a mixture of white and ultraviolet light and powered by a 12V battery) was used for attracting males which were then collected by hand. Females were caught by searching the ground using a flashlight, looking for signs of movement, or by excavating burrows. Field observations of behaviour were made with a red filter over the flashlight.

Live adults, brought into the laboratory for observations on communication, stridulation, mating, grooming and feeding, were kept in small vials or petri dishes (diameter 90 mm, height 20 mm) with the bottom lined with paper towel to provide

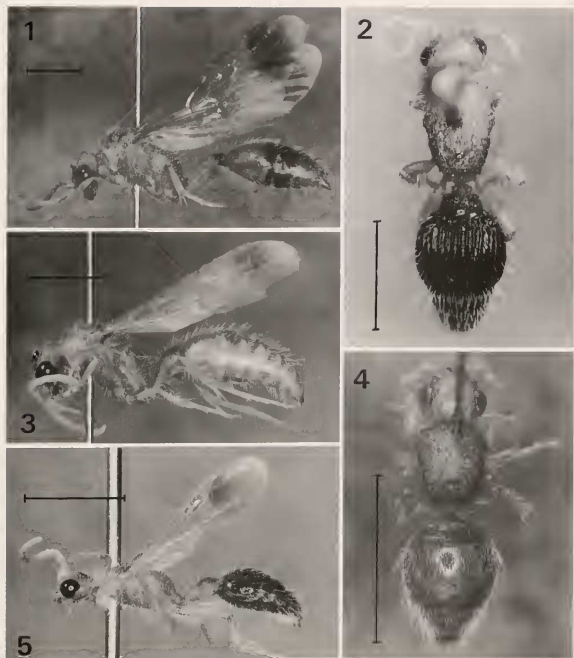
a rough substrate, in a dark cupboard, simulating conditions in natural refuges. A Wild M5 stereo microscope, using white light from a desk lamp, was utilised for laboratory observations at irregular intervals during the day and at night. Details on mating were obtained by placing two adults of opposite sex in the same petri dish. If no interactions (including stridulation or rubbing of antennae) occurred between them after several minutes, they were separated. The same two individuals were never placed together more than once, unless interactive behaviour between them had previously occurred. Grooming has not previously been described in mutillids, so grooming behaviour was noted in the field and the laboratory whenever seen, and detailed experimental observations were carried out after covering the body with flour. Observations (a total of at least 50) involved several specimens of all three species and the full repertoire of cleaning activities was seen in about 5 individuals of *T. thisbe* (including 1 female) and 8 of *T. imbellis*. The terminology used in the accounts of grooming is from Basibuyuk and Quicke (in litt.).

The accounts below apply to *T. thisbe* and *T. livida* unless otherwise stated.

RESULTS AND DISCUSSION

Habitat and Activity Patterns

Females are commonly associated with dry river beds, walking or running on the banks or in the adjacent loose vegetation. They walk slowly over hard compact soil, probing cracks and crevices with their antennae and regularly entering and leaving burrows. On loose sandy soil they move quickly without appearing to search. (Ferguson (1962) observed similar behaviour in females of the nocturnal subgenus *Photopsis* Blake.) When inactive, they hide in pre-existing burrows. Females were seen emerging from burrows with entrances opening on the vertical faces of banks of



Figs. 1-5. *Tricholabiodes* spp. 1, *T. thisbe*, ♂, lateral view. 2, *T. thisbe*, ♀, dorsal view. 3, *T. livida*, ♂, lateral view. 4, *T. livida*, ♀, dorsal view. 5, *T. imbellis*, ♂, lateral view. Scales = 3 mm.

compact soil and they were occasionally found when such burrows were excavated during the day.

Where the males reside during the day is unknown. At night, they were often seen entering and leaving small circular burrows but were never found residing in the burrows. Burrows and crevices that males were seen entering the previous night were excavated several hours later, but no males were found. They could not

be found in the surrounding vegetation along the riverbanks, under rocks, nor in neighbouring crevices or burrows. Males are hesitant to fly and prefer running with the wings folded above the metasoma. They fly in hops, landing every several metres. On cold (<20°C) evenings males were not seen, while on warm evenings, even with light drizzle, they were frequently found.

Based on specimen labels, individuals

of all southern African species of *Tricholabiodes* have been most frequently collected (and are probably most active) during the summer months (November to March); they are seldom active during early spring and late autumn, and never during winter (June to August). Although most species are strictly nocturnal, females of *T. thisbe* were sometimes observed active up to two hours before sunset. Since Nonveiller (1963) hypothesized that mutillids are generally stenothermic and thermophilic, these females may not be avoiding light, but are rather being active during optimum conditions of temperature, which usually occur only after sunset but on cool overcast days could occur several hours before sunset.

Females are not influenced by a stationary light. If a female enters the area illuminated by such a light, she continues her activities as if the light were not present. In contrast, females of *Photopsis* are positively phototropic (Ferguson 1962), and they usually approach the light in a semi-direct path, then move away into a shadow and remain motionless. Females of *Tricholabiodes* are startled by moving lights and either remain motionless for some time thereafter or show escape reactions.

Males could be collected only by attracting them to light; they have seldom been caught in malaise traps. It is thus probable that they are strictly nocturnal. Upon arriving at a light, they immediately entered the brighter inner circle of light before moving away and grooming themselves in the dimmer outer circle. The umbrella used in the light trap was divided into brown and white segments, with the white areas brighter than the brown. The males never rested on the white areas.

Predators and Defence

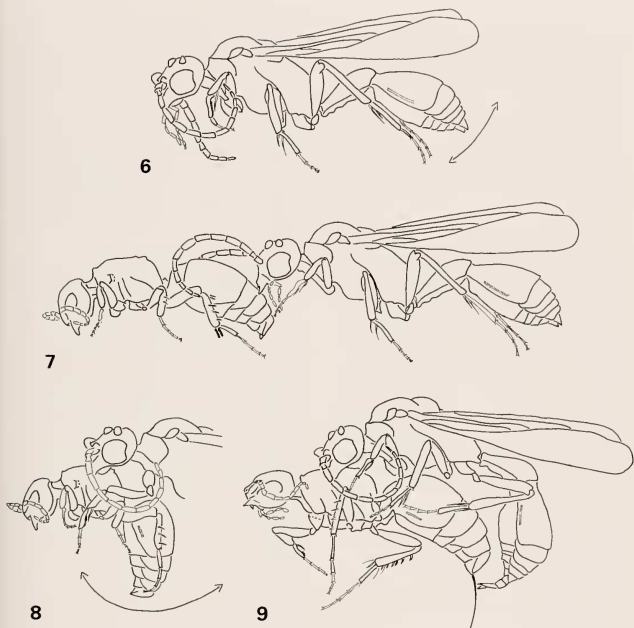
Females of *Tricholabiodes* appear to have relatively few enemies. Vertebrates were not observed eating them and they were ignored by invertebrates such as ants. The escape reaction used by the females in re-

sponse to disturbance tends to be species specific. When disturbed, females of *T. thisbe* entered the nearest convenient hole or crevice, but females of *T. livida* started burrowing. Female mutillids generally have a strongly sclerotized exoskeleton, especially the mesosoma which is robust. They also have potent stings and can bite (Masters 1979). When grasped, a female often stridulates and attempts to sting. A predator may thus become innately aware that sound and defence, i.e. sting, are often associated, and stridulation may aid predators in recognizing well defended mutillids in consequent encounters (Edmunds 1974).

Males of *Tricholabiodes* were seen being attacked and eaten by toads, birds (night-jar) and bats, and several species of ants. If attacked, males of *Tricholabiodes* stridulate and attempt to escape by flying or running. Stridulation is accompanied by opening and closing of the mandibles and flexing of the metasoma under the mesosoma, resembling the stinging motions of the female. Male mutillids are usually poorly protected against predators. If grasped, however, a male may administer a slight prick to a potential predator with the sharp parameres of the genitalia (Masters 1979). Masters (1979) further hypothesized that stridulation may also startle an attacker, thereby increasing the likelihood of escape by the mutillid, and noted that, in insects generally, stridulation is frequently coupled with other defences such as distasteful or noxious secretions. The stridulation and stinging motions of the male may thus trick the predator into assuming that he is well defended.

Mating

Tricholabiodes thisbe.—When a male and a female were confined to a petri dish after having been kept in separate vials ($n = 3$ pairs), they initially tried to escape. The male acted in an excited manner by attempting to fly and run randomly. Within a few seconds the members of the pair met



Figs. 6–9. *Tricholabiodes thisbe*, mating behaviour, diagrammatic. 6, antennal and metasomal movements of ♂ when sensing ♀. 7, antennal vibration by ♂ when contacting ♀. 8, ♀ resisting mounting attempt by ♂. 9, mating posture immediately before copulation.

at least once and whenever they met head-on neither member showed avoidance reactions. This is contrary to Ferguson's (1962) observations on *Photopsis* where he noted that whenever the two sexes met head-on both instantly showed avoidance or escape reactions by moving away in different directions. In *T. thisbe*, a male avoided a female only if she passed him from behind. Initially, when meeting, the male's antennae flickered continuously and his metasoma vibrated against the

base of the petri dish (fig. 6). His antennae then began to vibrate rapidly over the body of the female (fig. 7), and within seconds he attempted to mount her. The female resisted by stridulating strongly, flexing her metasoma so that the ventral surface touched her coxae (fig. 8), and used her mandibles to pry herself loose from him if he had not grasped her successfully.

The male grasped the female laterally at the mid length of the mesosoma with his

mandibles, and twisted his body so that both were lying on their sides. Her body was slightly arched with legs tucked under the mesosoma. His middle pair of legs rested laterally on her metapleuron, while the hind pair lay on the second tergum, near the felt line. Once the female was securely grasped, the male partly extruded his genitalia (fig. 9) and began prodding her genital opening at about one prod per second. At this point the female started stridulating softly. The duration of the prodding varied before copulation occurred, lasting about 5–15 seconds. Genital union lasted 10–15 seconds, during which her ovipositor was partly extruded, although the pair sometimes remained in the copulatory position for up to seven minutes. Immediately after genital union, the male released his hold and the pair separated. The way in which the apical segments were joined and the details of genitalic attachment could not be studied under the microscope as the slightest disturbance caused the pair to separate.

The entire copulation process occurred on the ground; no attempt was made by the male to fly with the female nor did the female, once firmly grasped by the male, try to dislodge him. Nonveiller (1963) stated that among individuals of similar size, mating takes place on the ground for it is not possible for the male to fly freely with the female. He observed *Smicromyrme jovanovici* Nonveiller mating in a position similar to that of *T. thisbe*, as does *Dasytilla foxi* (Cockerell) (Spangler & Manley 1978). *Pseudomethoca frigida* (Smith), in contrast, mates with the female standing and the male above her (Brothers 1972).

For several minutes after copulation, the female partly extruded and withdrew her sting every few seconds. Brothers (1972) suggested that these pumping movements may aid movement of the sperm into the spermatheca. The male withdrew his genitalia before settling down to groom himself. After several minutes, he often again mounted the female but the encounter

lasted only several seconds and never more than a minute, and actual copulation was never repeated. Subsequent encounters between the male and female were of shorter duration than the previous ones. The attractiveness of a mated female diminishes rapidly after mating, as has been observed in other species (Brothers, 1972). On one occasion a different male attempted to mount the already mated female and he spent several seconds prodding her with his genitalia before ceasing his activities.

Tricholabiodes livida.—Mating in *T. livida* ($n = 2$ pairs) is similar to that in *T. thisbe* except for a few details. The male grasped the female more towards the anterior margin of the scutum with his mandibles and used all three pairs of legs to hold the female firmly once the pair was lying on their sides. The female then arched her metasoma forward, directing it between her legs, before copulation occurred. The male thus also curved his metasoma far forward. This position was probably adopted because the female was relatively much smaller than the male (compared with *T. thisbe*). Additional observations of mating in *T. livida* are needed to verify the consistency of the arching of the metasoma. No subsequent matings by other males with the already mated female were observed. Similarly, the mated female lost all attractiveness to neighbouring males.

Stridulation

Stridulation in mutillids has been assigned various functions in the past, including that of intraspecific (Mickel 1928) and interspecific signalling (Masters 1979), but little or no hard evidence has been provided to support most of the suggested functions. During the present studies, stridulation by males and females of *Tricholabiodes* was observed during periods of distress, during copulation and as an apparent calling device. Sounds made while a wasp is on the ground could probably be sensed by others as vibrations through

the tarsi, but how individuals sense sounds produced by others during flight is unknown. Neither sex has any obvious specialized structures for sensing these vibrations.

Distress.—When grasped, both sexes stridulate vehemently. The sounds produced are loud, continuous and of long duration. They may function to startle predators and warn of possible stinging, as has been shown for other mutillids by Masters (1979).

During copulation.—The female stridulates as the male prods her genital opening with his genitalia. The sounds produced are loud and rhythmic. They are not as intense or continuous as those produced during distress, and their function is unknown. Reciprocal calling, whether by "honking" (vibration of the mesosoma and wings using the flight muscles) or stridulation, by the male during copulation was not observed, unlike the situation in *D. foxi* (Spangler & Manley 1978).

Apparent calling: Communication.—Males grouped together (3 in a petri dish) communicated by slow, barely audible stridulation (heard on 4 separate occasions over about one hour each when the laboratory was quiet). The sounds produced were not as intense as those made during periods of distress and were of short duration (≤ 2 seconds). Individuals did not stridulate simultaneously but sequentially. While stridulating they remained stationary with the metasomal sterna resting on the ground. Within an hour, 'conversations' between individuals occurred 20–30 times. The function of these calls is unknown.

Apparent calling: Courtship.—On at least 2 occasions, between about 21:00 and 22:00, males of *T. thisbe*, while flying, were heard stridulating in an area where females were known to be most common (confirmed by later investigation). These sounds were loud, audible up to several metres away, and of a continuous long duration. It is assumed that they had some

function in communication between the sexes. Sounds have an advantage over visual signals for nocturnal animals (Masters 1979), since visual signals are ineffective at night, whether intraspecifically or interspecifically. This could also explain why nocturnal mutillids, including *Tricholabiodes*, are dull coloured without the bright patterns commonly seen in diurnal species.

Grooming

There are no differences in cleaning techniques between the species observed (except for one detail involving the antennae) and none between the sexes (except for the wings). If it is extremely dirty an individual first cleans the posterior part of the body partially, otherwise grooming proceeds anteroposteriorly.

Head.—The antennae are cleaned first, using the antennal cleaners of the ipsilateral forelegs. All species display either single- or, more commonly, double-antenna scraping (the cleaning of only one or both antennae at the same time respectively). During cleaning, the leg is lifted over the antenna which is placed in and pulled through the antennal cleaner by tilting the head backwards and simultaneously moving the leg away from the head. Individuals of *T. thisbe* and *T. livida* first clean the antennae distally then sequentially more proximally by cleaning a longer section each time the antenna is pulled through, using short rapid strokes. In contrast, individuals of *T. imbellis* pull the entire antenna slowly through the antennal cleaner 3–4 times. The ipsilateral middle leg cleans the foreleg after several strokes of the antenna through the antennal cleaner. The surface of the head is combed postero-anteriorly, using both fore legs simultaneously, the basitarsi and calcaria acting as combs or brushes. The calcaria also clean the mandibles. The fore leg, after several sweeps of the head, is cleaned by one or both middle leg(s).

Body.—Cleaning of the dorsal surface of

the mesosoma was not seen. The fore legs, reflected back and bent at the femoro-tibial joint, rub the tarsi, tibiae and calcaria along the mesopleura using short rapid movements. The calcar is angled away from the basitarsus. The calcaria and basitarsi clean the sterna. After several sweeps of the mesosoma, the forelegs are cleaned. The metasoma is cleaned using the hind legs, either individually or simultaneously. An individual balances on its front two pairs of legs, with wings folded dorsally, with the entire body slightly dorsally arched, while the hind legs rub along the metasoma, using the basitarsi and spurs. The longer tibial spur is angled away from the tibia. The sides are groomed first, followed by the dorsal surface and then the sterna.

Legs.—The legs are cleaned sequentially, anterior to posterior. A foreleg is cleaned either by the ipsilateral middle leg or both middle legs simultaneously. In the former, both fore and middle legs rub against each other or the fore leg may pass between the spurs and basitarsus of the middle leg; in the latter, the fore leg passes behind the ipsi- or contralateral middle leg spurs or is placed between the basitarsi of both middle legs which rub against it. In *T. thisbe* and *T. livida* at least, the fore leg is not pulled past the tibial spurs in one quick motion but is cleaned first distally, and then sequentially more proximally, as for the antennae. The middle legs are groomed separately using the tibial spurs and basitarsi of both hind legs. Only in exceptional circumstances, where the middle leg is very dirty, does the other middle leg aid the hind legs in cleaning it. One hind leg combs and rubs the other hind leg, using the basitarsus and tibial spurs. This action is then reciprocated for the other hind leg.

Wings.—The left and right wings, like the antennae, are cleaned either separately or simultaneously, using the tibiae and basitarsi of the hind legs; the fore wings are cleaned before the hind wings. They

are not cleaned in their normal resting position, but are orientated ventrolateral to the metasoma. When cleaning the dorsal surface, the fore wing has the costal margin ventrally oriented and the dorsal surface facing outwards. The metatibia and metabasitarsus, remaining outside the wing, slowly comb the wing. After 3–4 strokes of the wing the hind leg is cleaned. The posterior margin of the fore wing is cleaned once the dorsal surface has been combed; it is gripped and pulled between the spurs and the basitarsus. Thereafter, the fore wing is orientated so that the costal margin is dorsally placed, the ventral surface faces outwards, and the hind wing lies obliquely lateral to and slightly below the fore wing. The ventral surface of the fore wing is cleaned similarly to the dorsal surface, the leg being between the fore and hind wings. The hind wing is cleaned in a sequence similar to the fore wing, the latter being adjusted in position to permit access to the former. When the wings of both sides are being cleaned simultaneously, the animal balances on its front and middle legs, and when cleaning the wings separately, the wasp shifts its weight, arching the mesosoma away and the metasoma towards the wing that is being cleaned.

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